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RAPTOR PREDATION ON ROCK PTARMIGAN (*Lagopus mutus*) IN THE CENTRAL CANADIAN ARCTIC

Richard C. Cotter[1] and David A. Boag[2]
Department of Zoology, University of Alberta, Edmonton, AB, Canada T6G 2E9

Christopher C. Shank
Department of Renewable Resources, Government of the Northwest Territories, Yellowknife, NWT, Canada X1A 2L9

Abstract.—We studied the nature and timing of raptor predation on a population of Rock Ptarmigan (*Lagopus mutus*) in the central Arctic of the Northwest Territories from 1987 to 1989. The density of Rock Ptarmigan at Windy Lake declined during the 3 years of the study from 5.8 to 3.5 to 2.8 birds per 100 ha. The number of nesting pairs of raptors within 10 km of Windy Lake also declined during this period from 9 to 10 to 5. Nesting raptors included Gyrfalcons (*Falco rusticolus*), Peregrine Falcons (*Falco peregrinus*) and Golden Eagles (*Aquila chrysaetos*). Common Ravens (*Corvus corax*) were also present. During the breeding seasons of 1988 and 1989, 15% of the adult breeding population of Rock Ptarmigan were depredated. There was no sex or age bias among Rock Ptarmigan killed, but a temporal bias was recorded over the course of the breeding season. Predation was the proximate cause of death for 91% of Rock Ptarmigan found dead over the three summers. Falcons accounted for 95% of all predation, the majority likely by Gyrfalcons.

Depredación por raptoras que victiman a las de la especie *Lagopus mutus* en el Ártico central canadiense

Extracto.—Hemos estudiado la naturaleza y época de la depredación causada por raptoras en una población de *Lagopus mutus* en el Ártico central de los Territorios del Noroeste canadiense, desde 1987 a 1989. La densidad de estas raptoras en Windy Lake declinó durante los tres años de estudio desde 5.8 (1987), a 3.5 (1988), y a 2.8 (1989) aves por 100 hect. El número de parejas raptoras nidificantes dentro de 10 km de Windy Lake también declinó durante este período desde 9 (1987), a 10 (1988), a 5 (1989). Las raptoras nidificantes incluyeron especies tales como *Falco rusticolus, F. peregrinus,* y *Aquila chrysaetos.* Los *Corvus corax* también estuvieron presentes. Durante las estaciones de reproducción de 1988 y 1989, el 15% de la población reproductora de las *L. mutus* fue depredada. No hubo parcialidad por sexo ó edad entre las *L. mutus* que fueron muertas, pero sí se registró una parcialidad temporal durante el curso de la estación reproductora. La depredación fue la causa más probable para la muerte de 91% de *L. mutus,* a las que se las encontró muertas en el curso de tres veranos. Los halcones contribuyeron con el 95% de toda la depredación, la que, al parecer, en su mayoría fue causada por *F. rusticolus.*

[Traducción de Eudoxio Paredes-Ruiz]

In most predator-prey studies, including those of raptors and grouse, emphasis has been placed on either the predator or the prey. For example, in northern Canada, Poole (1987) studied the ecology and food habits of Gyrfalcons (*Falco rusticolus*), a major predator of ptarmigan (*Lagopus* spp.), whereas Hannon and Gruys (1987) studied the impact of predation on Willow Ptarmigan (*L. lagopus*) by mammals and raptors. Although the respective studies provided much information on the diet of Gyrfalcons (Poole and Boag 1988) and levels and patterns of predation on ptarmigan (Hannon and Gruys 1987), neither study examined the numerical relationship between predators and prey. We report on the nature and timing of predation on Rock Ptarmigan in the same area where the diet and feeding behavior of Gyrfalcons (Poole and Boag 1988) and the interrelationships within the raptor guild were reported (Poole and Bromley 1988). Our specific objectives were to determine numerically which predators were involved in ptarmigan predation, their relative impact, the relative vulnerability of different

[1] Present address: Richard C. Cotter, 8506d 169 St., Edmonton, AB, T5R 2W9.
[2] Present address: David A. Boag, 6746 Amwell Drive, R.R. 1, Brentwood Bay, BC, V0S 1A0.

age and sex classes of Rock Ptarmigan, and the timing of predation relative to their annual cycle. We also examined the extent to which differences in these variables were related to seasonal and annual differences.

STUDY AREA

The study area, centered around Windy Lake, Northwest Territories (68°05'N 106°40'W), lies near the center of the Kilgavik study area used by Poole (1987) in his study of Gyrfalcons. The area consists of gently rolling tundra punctuated by small rock outcrops. The main geological features are granitic intrusions, and diabase dykes and sills (Fraser 1964). Lines of cliffs and blocks of rock rising above the surrounding terrain provide nesting ledges for Gyrfalcons, Peregrine Falcons (*Falco peregrinus*), Golden Eagles (*Aquila chrysaetos*), and Common Ravens (*Corvus corax*), the major avian predators of adult ptarmigan (Cramp and Simmons 1980, Poole 1987). For a description on the flora, fauna and climates of the region see Poole and Bromley (1988).

METHODS

We surveyed all known and potential raptor nest sites within the Kilgavik region studied by Poole and Bromley (1988) each spring (May–early June) in 1987–89 to determine occupancy status. Particular attention was given to the area within a 10 km radius of Windy Lake where, on two nearby study areas, most Rock Ptarmigan were captured and marked. Rock Ptarmigan were captured at the onset of the breeding season (early June) using a noose pole or ground nets (Hannon 1983). Sex and age were recorded for all individuals. Birds were classed as adult (≥1 yr old) or yearling (<1 yr old) based on the pigmentation of the eighth and ninth primaries (Parker et al. 1985). All birds were fitted with four color-coded bands: one numbered aluminum and three numbered plastic (National Band and Tag Co., Newport, KY).

In 1988 and 1989 all female Rock Ptarmigan were fitted with 12-g "necklace" radio transmitters (Biotrack, Wareham, U.K.). Only half of the males were fitted with radio transmitters; in 1988 with 18-g "backpack" radio transmitters (Telemetry Systems, U.S.A.) and in 1989 with 12-g "necklace" transmitters.

In 1987 work on ptarmigan ceased after banding was completed in mid-June. In 1988 and 1989 the fate of adult males and females was followed through to the end of each breeding season by regularly surveying (every 3–4 d) their respective territories. If an individual ptarmigan was not immediately visible, it was located by radio telemetry, or, in the case of males not radio-marked, by intensive searches of its territory.

When a ptarmigan was killed, we attempted to identify the predator from the location and nature of the ptarmigan remains. All remains were examined closely when the identity of the predator was not obvious at the kill site; a description of the location, date, and condition of the remains was recorded for comparison with descriptions in the literature for potential predator species involved (Einarsen 1956, Jenkins et al. 1964, Nielsen 1986). In some cases of presumed Gyrfalcon predation, identification was confirmed by the presence of either leg bands or radio at a nearby Gyrfalcon nest site or plucking post. Birds with transmitters that were killed by predators were found and their status documented. The fate of males without transmitters could not be ascertained in all cases, and the recorded number of males preyed upon during the breeding season is, therefore, a minimum. Predation rate was calculated as the percent of resident males or females, present at the onset of the breeding season, that were subsequently lost to predators.

Survival rates of banded ptarmigan were calculated using the Kaplan-Meier (K-M) product limit method, as modified by Pollock et al. (1989) for staggered entry of animals. Survival rates were calculated on a weekly basis. The K-M method calculates a survival function (S[t]) which is "the probability of an arbitrary animal in a population surviving t units of time from the beginning of the study" (Pollock et al. 1989). Ptarmigan, whose fate was known only up to a certain date, were eliminated from analysis from that date on (White and Garrot 1990). When dates of last observation and documented death spanned several days, a median date was used. Statistical differences in the survival function between age and sex groups were examined out using the most conservative of the three "approximate chi-square" tests presented by Pollock et al. (1989).

Data sets of observed frequencies were compared using 2 × 2 contingency analyses with the G-test of independence and Williams Correction (Sokal and Rohlf 1981). The significance level was $P < 0.05$ for all tests.

Table 1. Number of nesting pairs of raptors within 10 km of Windy Lake, Northwest Territories, in 1987–89.

SPECIES	1987	1988	1989
Gyrfalcon	3	4	2
Peregrine Falcon	3	3	2
Golden Eagle	1	1	0
Raven[a]	2	2	1
Total	9	10	5

[a] Considered as a "functional raptor" (White and Cade 1971)

RESULTS

The number of raptors nesting within 10 km of Windy Lake declined from 1987–89 (Table 1). Falcons comprised 71% of all nesting raptors with an almost equal number of Gyrfalcons and Peregrine Falcons (Table 1). There was also a decline in ptarmigan densities per 100 ha between 1987 and 1989; from 5.8 in 1987 to 3.5 in 1988 and to 2.8 birds in 1989.

Between June 1987 and July 1989, 96% (123/128) of resident Rock Ptarmigan were marked and released, the overall sex ratio favoring males (1:0.83; Table 2). The survival function (S[t]) of these birds over the breeding season (29 May to 31 July), for

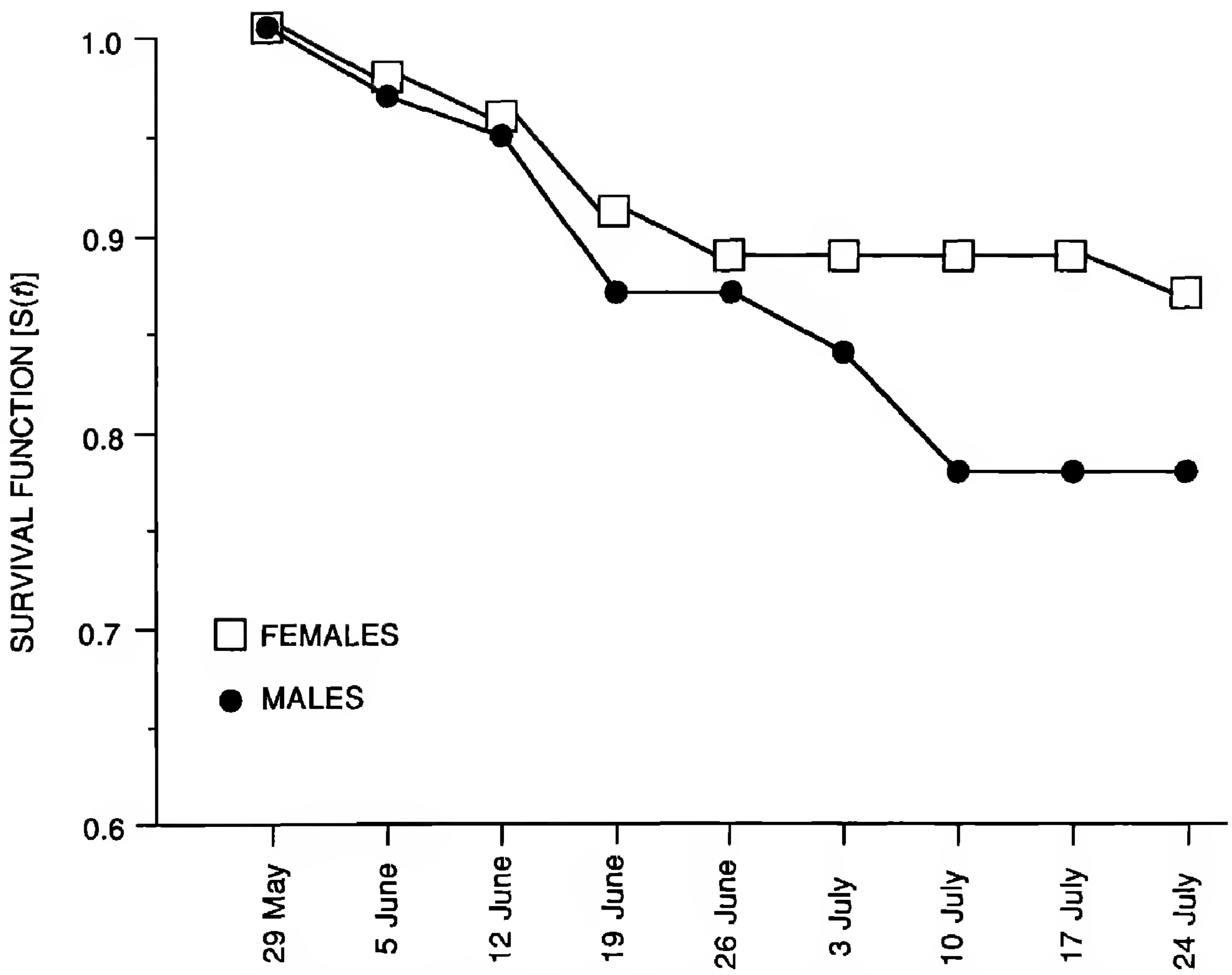

Figure 1. The Kaplan-Meier survival function (modified for staggered entry of animals) of male and female Rock Ptarmigan over the breeding seasons of 1988 and 1989 at Windy Lake, Northwest Territories.

1988 and 1989 combined, was 0.82. There were no differences between the sexes (Fig. 1; females 0.87, males 0.78, $\chi^2 = 0.08$, $P > 0.95$), or between age classes (adults 0.81, yearlings 0.84, $\chi^2 = 0.04$, $P = 0.84$). Eighteen percent of birds (23/128) resident for one or more breeding seasons were found dead. Mortality over the breeding season must be considered minimal because the fate of some birds was not known at the end of the season. Assuming that all of these birds died, either during the breeding season or before returning the following spring, annual mortality would rise to 57%, somewhat higher among females (61%) than males (50%).

Predation was the proximate cause of death in 21 of 23 ptarmigan found dead over the three summers. A predator was identified for all 21 depredated Rock Ptarmigan found on the study area. All but one of the birds were killed by falcons (Table 3). The other, a female, was taken by either Red (*Vulpes vulpes*) or Arctic fox (*Alopex lagopus*). During the study, falcons killed an equal number of males (10) and females (10). Seventeen of the 21 kills occurred during the breeding season, 1 occurred in autumn, and 3 occurred between mid-summer and winter (in 1987). The predation rate during the breeding season, all years combined, was 14% (6% in 1987, 15% in 1988, and 14% in 1989). Predation rate did not differ among years ($G = 0.61$, df = 2, $P = 0.74$). Based on data from 1988 and 1989, more Rock Ptarmigan were killed in June ($N = 14$) than in July ($N = 2$) ($G = 10.35$, df = 1, $P < 0.01$). There were no differences between the proportion of males and females killed in either June ($G = 0.50$, $P = 0.48$) or July ($G = 2.46$, $P = 0.12$). A comparison of all known raptor predation events from the breeding seasons of 1988 and 1989 revealed no difference ($G = 0.01$, df = 2, $P = 0.92$) between males (15%, $N = 61$) and females (14%, $N = 49$). There was also no difference in the percentage of adults (14%, $N = 63$) and yearlings (14%, $N = 42$) killed during the breeding seasons of 1988 and 1989 ($G = 0.00$, $P > 0.95$), and this was true for both males ($G = 0.24$, $P = 0.62$) and females ($G = 0.10$, $P = 0.75$).

DISCUSSION

The density of Rock Ptarmigan at the onset of the breeding season at Windy Lake declined over the course of this 3-year study. In the larger Kilgavik region, the pattern was similar, with the decline commencing in 1986 after 3 consecutive years of population increase (Poole and Boag 1988, Cotter 1991). The number of nesting raptors in the vicinity of Windy Lake declined from 1987-89 as well. The decline in numbers of breeding raptors, which coincided with that of the Rock Ptarmigan, suggests that these raptors assess food resources early in the season before beginning the reproductive cycle. However, Shank and Poole (1992) noted that in the larger Kilgavik region the number of productive Gyrfalcon pairs declined only slightly during those years, from 11 in 1987 to 9 in 1988, and with no change from 1988 to 1989. This discrepancy between Windy Lake and the larger Kilgavik region makes it difficult to understand whether this population of Gyrfalcons is responding to the changes in numbers of breeding ptarmigan. Court (1986) suggests that Peregrine Falcons often will hold territory early in the season but abandon it shortly thereafter and apparently forego reproduction in that year. Poole and Bromley (1988) observed among Gyrfalcons at Kilgavik that the percentage of territorial pairs to initiate laying ranged between 64 and 91%; however, regardless of the annual variation there were no differences between years in either mean brood size or productivity. The fact that those birds which did nest and produce young fledged normal numbers of chicks suggests that the precision with which food resources for breeding is measured is high.

It has been suggested that different mortality rates observed in male and female Rock Ptarmigan (Weeden and Theberge 1972) are a consequence of differences in conspicuousness of the sexes during the incubation phase of the breeding season (Bergerud and Mossop 1984). Prior to hatching, which in the Kilgavik region occurs in early July (Cotter 1991), females have been cryptic (both in plumage and behavior) for a period of 3-4 wk, whereas males have been cryptic for only a week or so (MacDonald 1970). In this study there was no sex bias in ptarmigan mortality over the course of the breeding seasons of 1988 and 1989, and this was true on a monthly basis (June and July) as well. Poole (1987) found similar proportions of each sex among prey remains taken from Gyrfalcon nest sites at Kilgavik during May-June and July-August of 1984-87. The lack of any sex bias in ptarmigan predation during the breeding season at Windy Lake and Kilgavik, particularly prior to hatching, indicates that in spite of differences in conspicuousness (and, therefore, perhaps vulnerability) of the sexes during the breeding season, falcons have equal success in taking male and female ptarmigan.

There was a temporal bias in levels of predation on Rock Ptarmigan over the course of the breeding season, with most predation having occurred in June and very little in July. There are few data from other studies on relative levels of predation during the breeding season; nevertheless, Nielsen (1986) and Poole (1987) both reported seasonal variations in the apparent vulnerability of ptarmigan to Gyrfalcon predation. Nielsen (1986) observed two seasonal peaks in vulnerability, the first during the territorial stage in the early part of the breeding season,

Table 2. Number of resident Rock Ptarmigan at the onset (approximately 1 June) of the breeding season at Windy Lake, Northwest Territories. A difference in number of males and females indicates unpaired individuals Enclosed in parentheses are percentage yearlings.

YEAR	SIZE OF STUDY SITE (ha)	MALES	FEMALES	TOTAL DENSITY[a] (BIRDS/ 100 ha)
1987	310	9 (33)	9 (67)	5.8
1988	1720	33 (42)	28 (46)	3.5
1989	1695	28 (7)	21 (70)	2.8

[a] 8% (10/128) of resident Rock Ptarmigan were outside of area used for calculating density.

Table 3. Number of known depredations on male and female Rock Ptarmigan at Windy Lake, Northwest Territories, in 1987-89.

		PREDATOR			
YEAR	SEX	GYRFALCON	PEREGRINE FALCON	FALCON SPP.[a]	FOX SPP.[b]
1987	Male	1	0	0	0
	Female	1	0	2	0
1988	Male	1	1	2	0
	Female	1	0	4	1
1989	Male	3	0	2	0
	Female	0	0	2	0

[a] Killed by either a Gyrfalcon or a Peregrine Falcon.
[b] Killed by either a Red or an Arctic fox.

and the second after the territorial system has collapsed and chicks are capable of sustained flight, commencing in late summer and lasting into early winter. The period in between coincides with a period in which ptarmigan are much more secretive and cryptic (MacDonald 1970). Poole (1987) reported a similar seasonal variation in Rock Ptarmigan use by Gyrfalcons at Kilgavik. He also observed an inverse correlation between the percentage of ptarmigan in the diet of Gyrfalcons and the availability of juvenile Arctic Ground Squirrels (*Spermophilus parryi*). At Windy Lake, juvenile ground squirrels emerged in early July (Poole 1987), and their emergence coincided with a sudden drop in the proportion of ptarmigan among the collected prey remains. Thus predation pressure on ptarmigan may reflect not only the relative vulnerability of other potential prey, but also their own behavior and crypticity. Adult male and female Rock Ptarmigan, some of which had previous breeding experience at Windy Lake, incurred losses similar to those of yearlings breeding for the first time. This suggests that any potential increased vulnerability of young birds is overcome by the time they return to the breeding grounds for the first time.

The importance of Rock Ptarmigan as prey within the arctic raptor community is evident, particularly to Gyrfalcons the range of which overlaps to a large extent the holarctic distribution of ptarmigan and the diet of which has a high percentage of ptarmigan (Bergerud and Mossop 1984, Poole and Boag 1988). At Kilgavik, adult Rock Ptarmigan are known to be preyed upon by Gyrfalcons, Peregrine Falcons and Golden Eagles, and ptarmigan remains have been found in raven nests (Poole and Bromley 1988). Although ravens may occasionally kill adult ptarmigan (Nielsen 1986), they also scavenge ptarmigan from Gyrfalcon caches (Poole and Bromley 1988). It is not surprising that Golden Eagles were not important predators as they rely on other prey for the bulk of their diet (Cramp and Simmons 1980, Poole and Bromley 1988). In the Kilgavik region, Gyrfalcons and Peregrine Falcons comprised over half the population of nesting raptors within 10 km of the Windy Lake study sites. It is, therefore, not surprising that these two falcons accounted for all Rock Ptarmigan killed by avian predators during the breeding season. It was not always possible to determine which falcon had made the kill from the remains found since both species handle prey in similar fashion (Jenkins et al. 1964, Cramp and Simmons 1980). Thus more than half the falcon kills could not be classified to species responsible. Even so, given that seven of eight kills, for which the species of falcon was known, were by Gyrfalcons suggests that most of the falcon kills were, in fact, by Gyrfalcon. In the central Canadian Arctic, therefore, Gyrfalcons would seem to be the most important predator of Rock Ptarmigan during the breeding season (see also Bergerud and Mossop 1984, Nielsen 1986, Poole 1987, and Gardarsson 1988).

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